# Alien and native plant establishment in grassland communities is more strongly affected by disturbance than above- and below-ground enemies



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| Journal: | *Journal of Ecology* |
| Manuscript ID | JEcol-2016-0094.R3 |
| Manuscript Type: | Standard Paper |
| Date Submitted by the Author: | n/a |
| Complete List of Authors: | Müller, Gregor; University of Konstanz, Ecology, Department of Biology<br>Horstmeyer, Lena; University of Konstanz, Ecology, Department of Biology<br>Rönneburg, Tilman; University of Konstanz, Ecology, Department of Biology<br>van Kleunen, Mark; University of Konstanz, Biology<br>Dawson, Wayne; University of Konstanz, Ecology Research Group; Durham University School of Biological and Biomedical Sciences, School of Biological and Biomedical Sciences |
| Key-words: | belowground interactions, biotic resistance, coexistence, community ecology, enemy release hypothesis, herbivory, invasion ecology, pathogens, plant-soil feedback, plant-soil (below-ground) interactions |

Dawson & Schrama Special Feature

# Alien and native plant establishment in grassland communities is more strongly affected by disturbance than above- and below-ground enemies

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## Summary

**1.** Understanding the factors that drive commonness and rarity of plant species, and whether these factors differ for alien and native species, are key questions in ecology. If a species is to become common in a community, incoming propagules must first be able to establish. The latter could be determined by competition with resident plants, the impacts of herbivores and soil biota, or a combination of these factors.

**2.** We aimed to tease apart the roles that these factors play in determining establishment success in grassland communities of 10 alien and 10 native plant species that are either common or rare in Germany, and from four families. In a two-year multi-site field experiment, we assessed the establishment success of seeds and seedlings separately, under all factorial combinations of low versus high disturbance (mowing vs mowing and tilling of the upper soil layer), suppression or not of pathogens (biocide application) and, for seedlings only, reduction or not of herbivores (net-cages).

**3.** Native species showed greater establishment success than alien species across all treatments, regardless of their commonness. Moreover, establishment success of all species was positively affected by disturbance. Aliens showed lower establishment success in undisturbed sites with biocide application. Release of the undisturbed resident community from pathogens by biocide application might explain this lower establishment success of aliens. These findings were consistent for establishment from either seeds or seedlings, although less significantly so for seedlings, suggesting a more important role of pathogens in very early stages of establishment after germination. Herbivore exclusion did play a limited role in seedling establishment success.

**4.** *Synthesis*: In conclusion, we found that less disturbed grassland communities exhibited strong biotic resistance to establishment success of species, whether alien or native. However, we also found evidence that alien species may benefit weakly from soil-borne enemy release, but that this advantage over native species is lost when the latter are also released by biocide application. Thus disturbance was the major driver for plant species establishment success and effects of pathogens on alien plant establishment may only play a minor role.

**Key-words:**

below-ground interactions, biotic resistance, coexistence, community ecology, enemy release hypothesis, herbivory, invasion ecology, pathogens, plant-soil feedback, plant–soil (below-ground) interactions

## Introduction

Disentangling the determinants that allow some species to establish successfully and spread while other species fail to do so is an important question in ecology. Germination and seedling survival are important steps in a plant's life cycle, and can have substantial impacts on plant population dynamics and consequently on species commonness. Establishment is a crucial step for a non-native species, in order to colonize new habitat and spread in a new range. While only few introduced species actually establish self-sustaining populations (Williamson & Fitter 1996), and most of those remain at low density (Ortega & Pearson 2005), some alien species possess the potential to dominate communities and reduce plant diversity (Vilà et al. 2011), and impact ecosystem processes (Liao et al. 2008; Vestergard, Ronn & Eklund 2015). Consequently, an improved understanding of what drives plant species establishment can help to explain patterns of community assembly (Seastedt & Pysek 2011) and dynamics of range expansions (Engelkes et al. 2008).

It has been proposed that the mechanisms explaining invasion success of alien species and commonness of native species may be the same, allowing both sets of species to achieve and maintain high abundances and a wide distribution (Thompson, Hodgson & Rich 1995: van Kleunen & Richardson 2007; Jeschke & Strayer 2008; van Kleunen et al. 2010a). For example, Dawson, Fischer & van Kleunen (2012) found that invasive alien and common native species do not respond fundamentally differently to nutrient addition and competition. Furthermore, invasive species can have similar characteristics as common native species do, such as short life cycles, fast germination and growth, superior dispersal abilities and high reproductive effort (Grotkopp & Rejmanek 2007; van Kleunen, Weber & Fischer 2010b; Dawson, Fischer & van Kleunen 2011). There is also ample evidence that removal of resident plants by disturbance can lead to greater recruitment of incoming species due to reduced competition or release of nutrients (Lozon & MacIsaac 1997; Hierro et al 2006; Questad &

Foster 2008; Myers & Harms 2009; MacDonald & Kotanen 2010; Maron et al. 2012; Kempel et al. 2013, but see Moles et al. 2012). For example, Meyers & Harms (2009) found in a meta-analysis on 28 studies that disturbance increases opportunities for species recruitment. Similarly, Hierro et al. (2006) identified disturbance as an important driver for success of *C. solstitialis* in its non-native range, while MacDonald & Kotanen (2010) found that disturbance increased establishment of *Ambrosia artemisiifolia* in its home range. These findings underline the role that disturbance can play for alien and native plant establishment success.

Although the drivers of commonness of natives and invasiveness of aliens may be partly the same, it is frequently argued that introduced non-native species may have gained an advantage over resident native species through leaving behind natural enemies (the “enemy release” hypothesis, Keane & Crawley 2002; Colautti et al 2004). If the inhibitory effect of an interaction with pathogens or herbivores is relaxed for an alien species in its introduced range, such enemy release may explain the disproportional success of some species in their introduced range (Klironomos 2002; Mitchel & Power 2003; Agrawal et al. 2005; Liu and Stiling 2006). In contrast, generalist antagonists in the introduced range may contribute to the biotic resistance of native communities against invaders (Elton 1958; Levine, Adler & Yelenik 2004; Parker, Burkepile & Hay 2006; Parker & Gilbert 2007 Pearson, Potter & Maron 2012). The “biotic resistance” hypothesis proposes that the community of local herbivores, pathogens and competitors provide resistance against invading species, specifically hindering establishment and suppressing growth of species that are not adapted to their mode of predation, infection or competition (Maron & Vilà 2001; Levine, Adler & Yelenik 2004). In particular, enemy release and biotic resistance may be caused by above *and* below-ground interactions (Agrawal et al. 2005; Morriën, Engelkes & van der Putten 2011; Vestergard, Ronn & Ekelund 2015), and while often considered separately, they may also act simultaneously to drive establishment success of alien and native plant species, but with different relative importance.

Despite increasing awareness of potential effects of multiple interacting factors such as enemy release, biotic resistance and disturbance on invasion success (Blumenthal 2006), there are few studies that test the relative importance of different factors experimentally (Hierro et al. 2006; Morriën, Engelkes & van der Putten 2011; Kempel et al. 2013; Maron et al 2013). In addition, we are not aware of any study that simultaneously assessed the relative roles of below-ground enemies (e.g. soil fungi), above-ground enemies (e.g. invertebrate herbivores) and disturbance in explaining establishment success of alien and native species in semi-natural communities.

In this study, we provide a novel test of the effects of disturbance, pathogens and herbivores on establishment success of 10 alien and 10 native herbaceous plant species sown from seed and planted as seedlings into grassland communities in southern Germany. Half of the species are considered common and the other half are rare in Germany. Specifically, we asked the following questions: 1) Does disturbance increase establishment success of incoming species, and do its effects differ between alien and native or common and rare species? 2) Does biocide treatment lower establishment success of incoming species due to release from pathogen pressure on the resident community, and does this affect aliens more than natives, as alien species may lose their potential competitive advantage? 3) Similarly, does release from herbivore pressure influence establishment success of the incoming species, and does this effect differ between alien and native or common and rare species? 4) Do the three factors disturbance, biocide treatment and herbivore reduction interact to affect plant establishment success?

## Materials and methods

*Target species*

In order to be able to generalize results beyond a few model species (van Kleunen et al. 2014), we conducted a multi-species field experiment using 20 different target species (biennial or perennial) from four different families (Table 1). The chosen target species represented taxonomic quadruplets that contained one common native, one rare native, one common alien and one rare alien plant species. As a proxy for the degree of commonness of each species, we used the number of 130-km$^2$ grid cells occupied by the species in Germany (maximum 3000) extracted from the FloraWeb database (FloraWeb, Bundesamt für Naturschutz, last accessed 8$^{th}$ June 2015). We also aimed to choose species that occur in similar habitats, excluding habitat specialists and species that are not simply rare due to their geographic distribution overlapping only marginally with the borders of Germany.

*Field sites and experimental setup*

The experimental setup consisted of five sites located in meadows surrounding the University of Konstanz, Germany. Four sites were located in Hockgraben, a local park that has been managed for its conservation value as a meadow landscape and is fertilized and mown annually. The fifth site was located in a meadow next to the Limnological Institute of the University of Konstanz (Appendix S1 Table A1 in Supporting Information).

Each site consisted of 12 plots of 12 m$^2$ (4 m x 3 m) each, arranged in a four-by-three grid and separated by 2 m wide paths (Appendix S1 Fig. A1). The grid of plots was surrounded by a one-metre wide boundary, resulting in a total site area of 360 m$^2$ (15 m x 24 m). Four of the 12 plots per site were used to test establishment success from seed ("seed-experiment plots”), and the other eight plots were used to test establishment success of pre-reared seedlings (“seedling-experiment plots”) (see “Seed experiment” and “Seedling experiment” subsections for details). This approach allowed us to assess whether the drivers of establishment success differ between the two early life stages. The positions of the seed and seedling plots were chosen randomly within each site.

*Seed experiment*

Every seed-experiment plot consisted of 160 subplots, distributed in two sets of five rows of 16 subplots, with a 50 cm wide path in between the two sets of five rows and a 40-45 cm gap to the edge of the plot (Appendix S1 Fig A2). Each subplot consisted of a ring cut from PVC tubes, with a height of 1 cm and a diameter of 5 cm. The ring was fixed in the ground with two nails. The centres of two neighbouring rings were 21 cm apart within the row, and 20 cm apart between two adjacent rows.

We randomly selected eight subplots per plot for each species, and sowed eight seeds of the respective species into each ring. A total of 1,280 seeds per species were sown across the whole experiment, resulting in 25,600 seeds in total. When the random selection resulted in more than two subplots of the same species next to each other, one or more of them were moved, to avoid an aggregation of one particular species in an area. Sowing took place from the 14$^{th}$ to the 16$^{th}$ of April 2014 (Appendix S1 Table A2).

The seed experiment consisted of a factorial design with a disturbance treatment (high/low) and a biocide treatment (biocide/water control). In each site, we applied each of the four treatment combinations to one of the four seed-experiment plots. For the low-disturbance treatment, plots were mown to 5 cm sward height (Appendix S1 Table A2). For the high-disturbance treatment, we tilled the plots after mowing and before the sowing of seeds (Appendix S1 Table A2) with a motorised rotary tiller to a depth of approximately 5-7 cm, and compacted the soil afterwards with a soil compactor, thus disturbing the local plant community and creating patches of open ground. For the biocide treatment, we treated plots alternatingly with Previcur Energy® and Fenomenal® (Both: Bayer CropScience AG, Monheim, Germany). Previcur Energy® acts against downy mildew and *Pythium* species, and propamocarb and fosetyl-aluminium are the active ingredients. Fenomenal® acts against soil-borne pathogens like *Pythium* and *Phytophthora* species (Oomycota), and fosetyl-aluminium and fenamidone are the active ingredients. Propamocarb and fosetyl are both systemic agents that are taken up through the root system and accumulate in the plant tissue, providing a curative effect and preventing infection for three to eight weeks. Previcur Energy® is used in agriculture and horticulture to treat pathogenic *Pythium* species and downy mildew in a wide range of vegetables and ornamental plants from different families. Due to the systemic mode of the biocides, they may also have an impact/effect on above-ground foliar pathogens (downy mildews). We applied one of the biocides alternatingly every six weeks during the growing season (see Appendix S1 Table A2). We followed the manufacturers' recommendations for the dosages of both biocides. For Previcur Energy®, we used 36 ml of the biocide dissolved in 36 L of water for each biocide plot. For Fenomenal®, we used 12 g dissolved in 16 L of water for each biocide plot receiving biocide treatment. Control plots received equivalent amounts of water instead. We surveyed the plots from the 2nd to the 17th of June 2014 in the first season for successful germination and establishment of the species (Appendix S1 Table A2).

*Seedling experiment*

We reared seedlings of all species in a greenhouse of the Botanical Garden of the University of Konstanz, starting with sowing on the 17th of March 2014 (Appendix S1 Table A2). Each tray (29 cm × 47 cm × 6 cm) contained roughly 500 seeds of one species in a standard substrate of peat and clay (Einheitserde Classic Profisubstrat Typ VM, Einheitserde- und Humuswerke Gebr. Patzer GmbH & Co. KG, Sinntal-Jossa, Germany). The light regime in the greenhouse was 12 h light/12 h dark. Temperatures were first between 18°C at night and a minimum of 20°C during the day. Then, to allow the plants to adjust to outside conditions, the temperatures were lowered on the 2nd of April to 7°C at night and external day temperatures during the day. One week later, the trays were placed outside until seedlings were transplanted. The plants were watered daily until transplanting into the field sites.

From the 17th to the 29th of April 2014 (Appendix S1 Table A2), we planted each of the eight seedling-experiment plots per site with 160 seedlings (20 species, 8 individuals per species) and marked the seedling positions with coloured wooden sticks. We used the same setup as for the seed experiment (Appendix S1 Fig. A2). With eight plots at each of five sites, a total of 6,400 plants were planted (320 per species). We used the same species as in the seed experiment, with one exception (Table 1). *Senecio jacobaea* showed signs of a disease infection when the seedlings were reared in the greenhouse, and therefore we replaced it with another common native Asteraceae *Eupatorium cannabinum*. In the analysis of the seedling-experiment, we finally used 5,839 plants, as 561 plants had to be excluded due to damage or mortality before all treatments were set up and all initial plant height measurements had been done.

The seedling experiment entailed the same disturbance and biocide treatments as the seed experiment described above. Additionally, because seedling survival may depend on invertebrate herbivores (molluscs and arthropods), we included a herbivore-reduction treatment, leading to a factorial design of the three treatments with eight plots per site. We assigned treatment combinations to plots, such that each treatment factor was represented in every row and column (if possible), including the plots used in the related seed experiment (Appendix S1 Fig. A1).

For the herbivore-reduction treatment, we built 1.8 m high cages with insect netting around each reduction plot. Because netting affects light levels, we built similar cages with insect netting containing large slits (see below) that allowed herbivores access as a control treatment. We anchored the wooden frames of the cages in the ground with metal base spikes, and stapled white insect netting (mesh size 0.8 mm x 0.8 mm, HADI Gartenbau, Marschacht, Germany) tightly on all sides and the top of the cages. For closed cages, we buried the insect netting c. 5 cm into the ground and secured it with nails into the ground. We made 80-cm wide closable doors in the netting by using Velcro®. In order to further reduce the presence of herbivores in the closed cages, we installed a yellow sticky trap (3.5m x 0.15m, IVOG® Midiroll, Sauter und Stepper, Ammerbuch, Germany) in the middle path at a height of c. 80 cm. In order to control emerging gastropods in the closed cages, we installed beer traps in two corners of each closed cage, and renewed them when necessary. Additionally, we placed a small amount of molluscicide (2 g Schneckenkorn Spiess-Urania, active ingredient metaldehyde, Spiess-Urania Chemicals GmbH, Hamburg, Germany) in the closed cages, immediately after they were built. For the open cages of the control plots, we had openings without netting instead of doors, and we left the lower 40 cm on all sides completely open. Furthermore, we cut a slit of 20 cm width on each side at a height of 100 – 120 cm, and removed the outer 30 cm of the two short sides of the ceiling. We prioritized the building of the closed cages of the herbivore-reduction plots, which took place between the 1st and 10th of May. The control plots received their open cages subsequently until the 20th of May.

We assessed survival of the seedlings (presence/absence) during three surveys; a first survey starting on the 5th of May 2014, a second survey in August 2014 and a final survey after the winter in April 2015 (Appendix S1 Table A2). During each survey, we additionally measured the height (highest point of the plant to the nearest 0.5 cm) and counted the number of fully expanded leaves of the target plants. Furthermore, we conducted additional experiments to test the effect of biocide on the resident plant community and to assess potential side effects of the biocide treatment on the mycorrhization of the plants. Moreover, we also tested for the effectiveness of the herbivore reduction cages (detailed information in Appendix S2 in Supporting Information). To assess the effects of the disturbance treatment on competitor removal we additionally recorded percentage cover of plants and bare ground in a 20 x 20 cm square centered on each target position from the 23rd to the 27th of June 2014 (Appendix S2). We also took soil samples in all plots of both the seed and seedling experiment to test for effects of the disturbance treatment on nutrient availability on the 22th of July 2014 (Appendix S2).

*Statistical analysis*

For the seed experiment, establishment success was quantified as the proportion of seeds that resulted in successfully established plants per subplot. Establishment success was analysed using a generalised linear mixed model of the beta-binomial family in the glmmADMB package (Fournier et al. 2012) in the software R 3.2.0 (R Core Team 2015). To account for taxonomic non-independence of species and for non-independence of the plots within each site, species nested in family and site were included as random effects. Disturbance (high/low), biocide (with/without), species origin (alien/native), species commonness (common/rare) and all interactions were included as fixed effects in a four-way interaction model. We used stepwise backward model selection *via* likelihood-ratio tests to obtain a minimum model, and to test for significance of interactions and main effects. We performed multiple pairwise comparisons to test for differences among levels of the terms in significant interactions or fixed effects using the 'multcomp' package (Hothorn, Bretz & Westfall 2008).

For the seedling experiment, we used generalised linear mixed effects models in the lme4 package (Bates et al. 2014) to analyse establishment success (i.e. survival). We used the optimizer "bobyqa" and set the maximum number of iterations to 100,000 to achieve model convergence. We analysed establishment success in the first year (2$^{nd}$ survey) and after the winter (3$^{rd}$ survey, Appendix S1 Table A2). Disturbance, biocide, herbivore reduction, species commonness and species origin were included as fixed terms in the model, as well as all possible interactions. Additionally, we included initial plant height and natural-log transformed number of leaves (both centred on the mean and scaled by the standard deviation) measured in the first survey after planting to correct for initial size differences. Species nested in family and plot nested in site were included as random effects. As for the seed experiment, we used stepwise backward model selection *via* likelihood-ratio tests to obtain a minimum model and to assess significance of the model terms. We also performed multiple pairwise comparisons to test for differences among levels of the terms in significant interactions or fixed effects using the 'multcomp' package.

Additionally, we analysed growth using the data on number of leaves and plant height from the first and second survey. We multiplied number of leaves with plant height to obtain a proxy for accumulated biomass of the plants (and to compensate for differences between growth forms e.g. rosette and non-rosette plants). We used this proxy to calculate the relative change in plant size, derived from the calculation for relative growth rate: Relative change in plant size = (ln(leaves * height 2$^{nd}$ survey) – ln(leaves * height 1$^{st}$ survey)) / (days 2$^{nd}$ survey- days 1$^{st}$ survey). Relative change in plant size was analysed using a linear mixed model with the same terms as the analysis described above. Similarly, we also used likelihood-ratio tests to assess significance of model terms and multiple pairwise comparisons to test for differences of levels among significant model terms.

## Results

### *Seed experiment*

The minimum model for establishment success from seeds retained a significant three-way interaction between disturbance, species origin and commonness, and a significant two-way interaction between biocide treatment and species origin (Table 2, Appendix S1 Table A3). Multiple comparisons showed that disturbance promoted establishment success of all groups of species. However, as indicated by the significant disturbance x origin x commonness interaction (Table 2, Appendix S1 Table A3), the magnitude of the disturbance effect depended on origin and commonness of the species. Among common species, the disturbance effect was stronger for natives (mean difference = 1.024, SE = ±0.108, P <0.001, Appendix S1 Fig. A3) than for aliens (0.776, SE = ±0.128, P <0.001), whereas, among rare species, it was stronger for aliens (1.850, SE = ±0.178, P <0.001) than for natives (0.782, SE = ±0.108, P <0.001, Fig. 1). The establishment success for alien species from seeds under biocide treatment was lower than under the control treatment (-0.430, SE = ±0.109, P < 0.001), but similar for native species (0.004, SE = ±0.076, P = 1, Fig. 2). However, the effect size of this difference is relatively small with 1.2 % lower probability of establishment for aliens under biocide treatment.

### *Seedling experiment*

The minimum model for establishment success from seedlings in the first growing season retained a significant 3-way interaction between biocide treatment, disturbance treatment and species origin (Table 3, Appendix S1 Table A4). Initial number of leaves was kept as a significant covariate in the model, indicating that larger seedlings had a higher probability of successful establishment (Table 3, Appendix Table A4). Overall, establishment from seedlings tended to be increased in the disturbance plots (Fig. 3), but as indicated by the significant biocide x disturbance x origin interaction, the strength and significance of the disturbance effect differed between the native and alien species, dependent on the biocide treatment. When plots were treated with the water control, the alien species did not benefit significantly from disturbance (0.584, SE = ±0.345, $P = 0.460$, Appendix S1 Fig. A4) whereas the native species did (0.989, SE = ±0.340, $P = 0.028$, Fig. 3). However, when plots were treated with biocide, both the alien species (mean difference =1.558, SE = ±0.348, $P < 0.001$) and the native species (1.380, SE = ±0.341, $P < 0.001$) benefitted similarly from disturbance (Fig. 3).

The minimum model for establishment success of seedlings in spring of the 2nd growing season contained a significant 3-way interaction between disturbance treatment, species commonness and species origin, another between biocide, herbivory and origin, and the significant main effects of initial height and number of leaves (Appendix S1 Table A5 and Table A6). Multiple comparisons showed that disturbance promoted establishment success of all groups of species. However, as indicated by the significant disturbance x origin x commonness interaction (Appendix S1 Table A5 and A6), the magnitude of the disturbance effect depended on origin and commonness of the species. Among common species, the disturbance effect was stronger for aliens (mean difference = 2.355, SE= ±0.277, $P < 0.001$, Appendix S1 Fig. A5) than for natives (1.584, SE = ±0.248, $P < 0.001$), whereas, among rare species, it was stronger for natives (3.480, SE= ±0.483, $P < 0.001$) than for aliens (2.232, SE = ±0.0.306, $P < 0.001$, Fig. 4). As indicated by the significant biocide x herbivory x origin interaction (Appendix S1 Table A5 and A6), responses of alien and native species to the herbivore-reduction treatment depended on biocide application. While establishment success of native species in herbivory-reduction cages was slightly higher in plots without biocide, alien species showed a slightly increased establishment success in herbivory-reduction cages only in plots treated with biocide. However, none of these effects was significant when we corrected for multiple tests (Appendix S1 Fig. A5).

The minimum model for relative change in plant size in the first season retained a significant 4-way interaction between disturbance, herbivory, commonness and species origin (Appendix S1 Table A7 and A8), as well as a 3-way interaction between biocide treatment, disturbance and herbivory (Appendix S1 Table A7 and A8), and another between biocide treatment, herbivory and species origin (Appendix S1 Table A7 and A8). The high disturbance treatment showed an overall positive effect on plant species size across all other treatments, with only little variation between common and rare or alien and native species (Appendix S1 Fig. A7). This clear effect of disturbance is corroborating the results from the survival models. Furthermore, rare native species performed worse than rare alien species in closed cages under high disturbance treatment (Appendix S1 Fig. A7).



## Discussion

In our multi-factorial field study, we tested whether disturbance, pathogens and herbivores influenced the establishment success from seed and seedlings of common and rare alien and native species. We found that disturbance was the most important driver of establishment success for both alien and native species, and also for both seed and seedling stages. This highlights that biotic resistance by a resident plant community is a major filter for incoming species (Levine, Adler & Yelenik 2004). Apart from the strong effect of disturbance, our results also reveal a minor role for pathogens, as seedlings of alien species showed lower establishment success in undisturbed sites with biocide application. In addition, alien species also showed lower establishment success from seeds when treated with biocide. This indicates that alien species may lose any competitive advantage when the resident community is also released from pathogen pressure (see also Reinhart & Callaway 2004, Reinhart et al. 2005). Notably, we did not observe clear effects of above-ground herbivore reduction on species establishment success in our experiment. This suggests that, in contrast with findings of greenhouse-based studies (Engelkes et al. 2008; Morrien, Engelkes & van der Putten 2011) interactions with pathogens may be more important than those with herbivores for establishment success.

The strong effects of disturbance leading to increased establishment as well as higher relative change in plant size can be linked to a reduction of competition (see Appendix S2; percentage cover) rather than altered nutrient availability (see Appendix S2; $NO_2^-$/$NO_3^-$ analysis). The role of disturbance as an important driver of establishment success is in line with numerous other studies (Hierro et al. 2006; Questad & Foster 2008; Myers & Harms 2009; MacDonald & Kotanen 2010; Maron et al. 2012; Kempel et al. 2013). For example, Kempel et al (2013) found that disturbance generally increased establishment success across a set of 93 alien and native plant species, but the importance of disturbance decreased over time relative to other factors (e.g. resistance against herbivores, species origin). Moreover, they found that native species showed a higher establishment success than aliens. In our experiment, native and alien species strongly profited from disturbance, but while native species also tended to show a higher establishment than alien species, a significant difference was only observed for rare aliens (compared to rare natives) under low disturbance, in the seed experiment. This suggests that rare alien species specifically suffer from competition with the intact resident community at initial establishment stages. The positive effect of disturbance on establishment success has also been observed by Radford, Dickinson & Lord

(2010) in a study on *Hieracium lepidulum* in New Zealand. However, Radford, Dickinson & Lord (2010) argue that (low) nutrient levels may be more important for *Hieracium* persistence after initial establishment. These findings point out that disturbance acts as a major factor for plant species establishment and strongly increases the likelihood that incoming species can overcome biotic resistance from a resident community (Lozon and MacIsaac 1997, Levine, Adler & Yelenik 2004). However, while the magnitude of the response to disturbance depended on origin and commonness of the species, overall both native and alien species benefited from disturbance with regard to establishment success as well as growth.

Besides the dominant role of disturbance, we also observed a small effect of biocide application on establishment success. Alien species established significantly worse from seeds when treated with biocide than native species. For seedlings, biocide application led to a similar decrease in establishment success from high to low disturbance for both aliens and natives. However, under the control treatment native species also showed a significant decrease from high to low disturbance, whereas alien species did not. Alien species may have lost their initial advantage of pathogen release relative to the resident plant community when the resident community is also released from pathogens because of biocide application. Consequently, greater competition with the resident community could explain the lower establishment success of alien species under low disturbance. We found a marginally non-significant increase in biomass for the community under biocide treatment (Appendix S2), which likely corresponds to a stronger competitive environment. As competitor removal was the likely driver behind the strong effects of disturbance, the slight increase in biomass accumulated by the resident community due to the biocide treatment is in line with the minor role that pathogen removal plays in reducing species establishment success.

Although the biocides used are specific against certain groups of pathogens (i.e oomycetes), it could be that the biocide had side effects on other organisms. We can exclude side effects of the biocide treatment on mycorrhiza (Appendix S2), which indicates that differences in establishment success due to biocide were not driven by side effects on an important group of soil mutualists. However, we cannot fully rule out that biocide did not affect abiotic soil properties or other soil organisms. However, we could also exclude an effect of the biocide treatment on nitrogen availability (Appendix S2) Notwithstanding this, our results indicate that the effects of disturbance and competition from resident communities on establishment success can also be influenced by pathogens, and that these mediatory effects depend on plant origin, likely *via* release of aliens from pathogens.

Contrary to the first growing season, survival of both alien and native species tended to be slightly higher in closed than open cages. Nevertheless, this herbivore-reduction effect was small and not significant. However, a large proportion of the plants surviving until the second growing season were from the Onagraceae (54 %). When we excluded the Onagraceae from the analysis, the results showed a significantly higher survival for common natives when growing in closed cages and generally a higher survival of common natives compared to rare natives in both open and closed cages (Appendix S3). In contrast, we found no significant differences for non-Onagraceae aliens. These findings indicate that the effects of herbivory showed large family-specific differences, with limited influence of the herbivory treatment on the Onagraceae potentially explaining the absence of an overall herbivore-reduction effect across all species. In another field experiment, Engelkes et al. (2016) found that herbivory reduced plant biomass and could influence which species dominated in a community, but they did not find that herbivory selectively promoted establishment of alien or native species. Evidence on the role of herbivory in plant species success from field and common garden studies remains equivocal (Blaney & Kotanen 2001; Agrawal & Kotanen

2003; Dostál et al 2013; Dawson et al. 2014; Engelkes et al. 2016; Korell et al. 2016). The lack of clear herbivore-reduction effects observed in our study corroborates these previous findings.

In summary, our study highlights the importance of assessing multiple potentially interacting factors that can contribute to establishment success of incoming alien and native plant species in existing plant communities. Disturbance had a strong effect on establishment success for both alien and native plant species, highlighting the suppressive effect of intense competition with the resident community for incoming species. Herbivory, in contrast, did not have a clear impact on species establishment success. However, we found evidence that the effects of disturbance can also be mediated by pathogens at both seed and seedling stages of establishment, and depending on species origin. Although the biocide effects in our study were small, alien species still may profit from pathogen release in intact grassland, but this benefit is lost when pathogens are suppressed and the resident community increases in biomass. This, and the overall difference in establishment success between alien and native establishment success supports the recent assertion that plant origin can matter when considering the drivers of alien species establishment and invasion (Buckley & Catford 2016). To conclude, our study shows that disturbance is a major driver for establishment success of incoming species, and interactions with pathogens can, to a lesser degree influence the level of biotic resistance of native communities to alien species.

## Acknowledgements

G.M. and W.D. were funded by the Deutsche Forschungs Gemeinschaft (Project DA 1502/1-1). We thank O.Ficht, Sina Glöckner, Timo Scheu and Marisa Braun for horticultural assistance and practical help. Thanks also go to the International Max Planck Research School for Organismal Biology for supporting G.M.

## Data accessibility

Data associated with this paper is available form Dryad Digital Repository (Müller et al. 2016)

## References

Agrawal, A.A. & Kotanen, P.M. (2003) Herbivores and the success of exotic plants: a phylogenetically controlled experiment. *Ecology Letters*, **6**, 712-715.

Agrawal, A.A., Kotanen, P.M., Mitchell, C.E., Power, A.G., Godsoe, W. & Klironomos, J. (2005) Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. *Ecology*, **86**, 2979-2989.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) lme4: Linear mixed-effects models using Eigen and S4_. R package version 1.1-7, <URL: http://CRAN.R-project.org/package=lme4>.

Blaney, C.S. & Kotanen, P.M. (2001) Post-dispersal losses to seed predators: an experimental comparison of native and exotic old field plants. *Canadian Journal of Botany-Revue Canadienne De Botanique*, **79**, 284-292.

Blumenthal, D.M. (2006) Interactions between resource availability and enemy release in plant invasion. *Ecology Letters*, **9**, 887-895.

Buckley Y.M., & Catford J. (2016) Does the biogeographic origin of species matter? Ecological effects of native and non-native species and the use of origin to guide management. *Journal of Ecology*, **104**, 4-17.

Bundesamt für Naturschutz, FloraWeb. - Available: http://www.floraweb.de, Accessed June 8$^{th}$ 2015.

Colautti, R.I., Ricciardi, A., Grigorovich, I.A. & MacIsaac, H.J. (2004) Is invasion success explained by the enemy release hypothesis? *Ecology Letters*, **7**, 721-733.

Dawson, W., Bottini, A., Fischer, M., van Kleunen, M. & Knop, E. (2014) Little evidence for release from herbivores as a driver of plant invasiveness from a multi-species herbivore-removal experiment. *Oikos*, **123**, 1509-1518.

Dawson, W., Fischer, M. & van Kleunen, M. (2011) The maximum relative growth rate of common UK plant species is positively associated with their global invasiveness. *Global Ecology and Biogeography*, **20**, 299-306.

Dawson, W., Fischer, M. & van Kleunen, M. (2012) Common and rare plant species respond differently to fertilisation and competition, whether they are alien or native. *Ecology Letters*, **15**, 873-880.

Dostal, P., Allan, E., Dawson, W., van Kleunen, M., Bartish, I. & Fischer, M. (2013) Enemy damage of exotic plant species is similar to that of natives and increases with productivity. *Journal of Ecology*, **101**, 388-399.

Elton, C.S. (1958) The ecology of invasions by animals and plants. The University of Chicago Press, Chicago.

Engelkes, T., Meissner, A., Morrien, E., Kostenko, O., Van der Putten, W. H. & Macel, M. (2016) Herbivory and dominance shifts among exotic and congeneric native plant species during plant community establishment. *Oecologia*, **180**, 507-517.

Engelkes, T., Morrien, E., Verhoeven, K.J.F., Bezemer, T.M., Biere, A., Harvey, J.A., McIntyre, L.M., Tamis, W.L.M. & van der Putten, W.H. (2008) Successful range-expanding plants experience less above-ground and below-ground enemy impact. *Nature*, **456**, 946-948.

Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M., Nielsen, A. & Sibert, J. (2012) AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software*, **27**, 233-249.

Grotkopp, E. & Rejmanek, M. (2007) High seedling relative growth rate and specific leaf area are traits of invasive species: Phylogenetically independent contrasts of woody angiospernis. *American Journal of Botany*, **94**, 526-532.

Hierro, J.L., Villarreal, D., Eren, O., Graham, J.M. & Callaway, R.M. (2006) Disturbance facilitates invasion: The effects are stronger abroad than at home. *The American Naturalist*, **168**, 144-156.

Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous Inference in General Parametric Models. *Biometrical Journal* **50**, 346—363.

Jeschke, J.M. & Strayer, D.L. (2008) Are threat status and invasion success two sides of the same coin? *Ecography*, **31**, 124-130.

Keane, R.M. & Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, **17**, 164-170.

Kempel, A., Chrobock, T., Fischer, M., Rohr, R.P. & van Kleunen, M. (2013) Determinants of plant establishment success in a multispecies introduction experiment with native and alien species. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 12727-12732.

Klironomos, J.N. (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature*, **417**, 67-70.

Korell, L., Stein, C., Hensen, I. Bruelheide, H., Suding, K. N. & Auge, H. (2016) Stronger effect of gastropods than rodents on seedling establishment, irrespective of exotic or native plant species origin. *Oikos*, in press.

Levine, J.M., Adler, P.B. & Yelenik, S.G. (2004) A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters*, **7**, 975-989.

Liao, C.Z., Peng, R.H., Luo, Y.Q., Zhou, X.H., Wu, X.W., Fang, C.M., Chen, J.K. & Li, B. (2008) Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytologist*, **177**, 706-714.

Liu, H. & Stiling, P. (2006) Testing the enemy release hypothesis: a review and meta-analysis. *Biological Invasions*, **8**, 1535-1545.

Lozon, J.D. & Macisaac, H.J. (1997) Biological invasions: Are they dependent on disturbance? *Environmental Reviews*, **5**, 131-144.

MacDonald, A.A.M. & Kotanen, P.M. (2010) The effects of disturbance and enemy exclusion on performance of an invasive species, common ragweed, in its native range. *Oecologia*, **162**, 977-986.

Maron, J.L., Pearson, D.E., Potter, T. & Ortega, Y.K. (2012) Seed size and provenance mediate the joint effects of disturbance and seed predation on community assembly. *Journal of Ecology*, **100**, 1492-1500.

Maron, J.L. & Vila, M. (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos*, **95**, 361-373.

Maron, J.L., Waller, L.P., Hahn, M.A., Diaconu, A., Pal, R.W., Muller-Scharer, H., Klironomos, J.N. & Callaway, R.M. (2013) Effects of soil fungi, disturbance and propagule pressure on exotic plant recruitment and establishment at home and abroad. *Journal of Ecology*, **101**, 924-932.

Mitchell, C.E. & Power, A.G. (2003) Release of invasive plants from fungal and viral pathogens. *Nature,* **421**, 625-627.

Moles, A.T., Flores-Moreno, H., Bonser, S.P., Warton, D.I., Helm, A., Warman, L., Eldridge, D.J., Jurado, E., Hemmings, F.A., Reich, P.B., Cavender-Bares, J., Seabloom, E.W., Mayfield, M.M., Sheil, D., Djietror, J.C., Peri, P.L., Enrico, L., Cabido, M.R., Setterfield, S.A., Lehmann, C.E.R. & Thomson, F.J. (2012) Invasions: the trail behind, the path ahead, and a test of a disturbing idea. *Journal of Ecology*, **100**, 116-127.

Morrien, E., Engelkes, T. & van der Putten, W.H. (2011) Additive effects of aboveground polyphagous herbivores and soil feedback in native and range-expanding exotic plants. *Ecology*, **92**, 1344-1352.

Müller, G., Horstmeyer, L., Rönneburg, T., van Kleunen, M. & Dawson, W. (2016) Data from: Alien and native plant establishment in grassland communities is more strongly affected by disturbance than above- and below-ground enemies. *Dryad Digital Repository*, doi: 10.5061/dryad.k6t16

Myers, J.A. & Harms, K.E. (2009) Seed arrival, ecological filters, and plant species richness: a meta-analysis. *Ecology Letters*, **12**, 1250-1260.

Ortega, Y.K. & Pearson, D.E. (2005) Weak vs. strong invaders of natural plant communities: Assessing invasibility and impact. *Ecological Applications,* **15**, 651-661.

Parker, I.M. & Gilbert, G.S. (2007) When there is no escape: The effects of natural enemies on native, invasive, and noninvasive plants. *Ecology*, **88**, 1210-1224.

Parker, J.D., Burkepile, D.E. & Hay, M.E. (2006) Opposing effects of native and exotic herbivores on plant invasions. *Science*, **311**, 1459-1461.

Pearson, D.E., Potter, T. & Maron, J.L. (2012) Biotic resistance: exclusion of native rodent consumers releases populations of a weak invader. *Journal of Ecology*, **100**, 1383-1390.

Questad, E.J. & Foster, B.L. (2008) Coexistence through spatio-temporal heterogeneity and species sorting in grassland plant communities. *Ecology Letters*, **11**, 717-726.

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Radford, I.J., Dickinson, K.J.M. & Lord, J.M. (2010) Does disturbance, competition or resource limitation underlie *Hieracium lepidulum* invasion in New Zealand? Mechanisms of establishment and persistence, and functional differentiation among invasive and native species. *Austral Ecology*, **35**, 282-293.

Reinhart, K.O. & Callaway, R.M. (2004) Soil biota facilitate exotic Acer invasions in Europe and North America. *Ecological Applications,* **14,** 1737-1745.

Reinhart, K.O., Royo, A.A., Van der Putten, W.H. & Clay, K. (2005) Soil feedback and pathogen activity in *Prunus serotina* throughout its native range. *Journal of Ecology,* **93,** 890-898.

Seastedt, T.R. & Pysek, P. (2011) Mechanisms of Plant Invasions of North America and European Grasslands. *Annual Review of Ecology, Evolution, and Systematics, Vol 42* (eds D.J. Futuyma, H.B. Shaffer & D. Simberloff), pp. 133-153. Annual Reviews, Palo Alto.

Thompson, K., Hodgson, J.G. & Rich, T.C.G. (1995) Native and alien invasive plants: More of the same*? Ecography*, **18**, 390-402.

van Kleunen, M., Dawson, W., Bossdorf, O. & Fischer, M. (2014) The more the merrier: Multi-species experiments in ecology. *Basic and Applied Ecology*, **15**, 1-9.

van Kleunen, M., Dawson, W., Schlaepfer, D., Jeschke, J.M. & Fischer, M. (2010a) Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. *Ecology Letters*, **13**, 947-958.

van Kleunen, M. & Richardson, D.M. (2007) Invasion biology and conservation biology: time to join forces to explore the links between species traits and extinction risk and invasiveness. *Progress in Physical Geography*, **31**, 447-450.

van Kleunen, M., Weber, E. & Fischer, M. (2010b) A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, **13**, 235-245.

Vestergard, M., Ronn, R. & Ekelund, F. (2015) Above-belowground interactions govern the course and impact of biological invasions. *AoB PLANTS,* **7**.

Vila, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarosik, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y. & Pysek, P. (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, **14**, 702-708.

Williamson, M. & Fitter, A. (1996) The varying success of invaders. *Ecology*, **77**, 1661-1666.

**Supporting Information**

Additional supporting information may be found in the online version of this article.

Appendix S1. Supporting information on experimental setup and model selection

Appendix S2. Additional experiments to test for the effects of the applied treatments

Appendix S3. Additional analysis excluding the Onagraceae

**Table 1**. The study species and their respective commonness, measured as the number of ~130 km$^2$ grid cells occupied in Germany out of a maximum of 3000 grid cells (FloraWeb, Bundesamt für Naturschutz), listed by family and origin.

| Family | Alien | | | Native | | |
|---|---|---|---|---|---|---|
| | **Species** | **Commonness** | **Grid cells** | **Species** | **Commonness** | **Grid cells** |
| Asteraceae | | | | | | |
| | *Aster novi-belgii* | common | 1530 | *Achillea millefolium* | common | 2741 |
| | *Solidago canadenis* | common | 2660 | *Senecio jacobaea*† | common | 2773 |
| | *Aster lanceolatus* | rare | 702 | *Eupatorium cannabinum*† | common | 2778 |
| | *Solidago graminifolia* | rare | 43 | *Aster amellus* | rare | 493 |
| | | | | *Achillea nobilis* | rare | 299 |
| Brassicaceae | | | | | | |
| | *Diplotaxis tenuifolia* | common | 1168 | *Cardamine pratensis* | common | 2923 |
| | *Lepidium heterophyllum* | rare | 98 | *Lepidium graminifolium* | rare | 86 |
| Caryophyllaceae | | | | | | |
| | *Cerastium tomentosum* | common | 1296 | *Silene latifolia* | common | 2893 |
| | *Gypsophila paniculata* | rare | 122 | *Silene viscosa* | rare | 9 |
| Onagraceae | | | | | | |
| | *Oenothera biennis* | common | 2591 | *Epilobium tetragonum* | common | 2468 |
| | *Oenothera glazioviana* | rare | 879 | *Epilobium dodoneii* | rare | 136 |

†*Senecio jacobaea* was only used in the seed experiment, and *Eupatorium cannabinum* was only used in the seedling experiment.

**Table 2.** Minimum generalized linear mixed effects model for probability of establishment success from seeds of 20 alien and native rare and common plant species under high and low disturbance treatment and biocide or water control treatment.

| **Parameters** | **Estimate (Std. error)** | **t-value** | **p-value** |
|---|---|---|---|
| *Fixed Effects* | | | |
| Intercept | -2.390 (0.368) | -6.49 | <0.001 |
| Disturbance (low) | -0.755 (0.127) | -5.95 | <0.001 |
| Biocide (yes) | -0.303 (0.092) | -3.30 | <0.001 |
| Origin (native) | 0.596 (0.495) | 1.20 | 0.228 |
| Commonness (rare) | 0.040 (0.495) | 0.08 | 0.935 |
| Disturbance (low) : Origin (native) | -0.269 (0.167) | -1.61 | 0.107 |
| Biocide (yes) : Origin (native) | -0.302 (0.117) | 2.58 | 0.009 |
| Disturbance (low) : Commonness (rare) | -1.029 (0.212) | -4.84 | <0.001 |
| Origin (native) : Commonness (rare) | -0.150 (0.695) | -0.22 | 0.829 |
| Disturbance (low) : Origin (native): Commonness(rare) | 1.271 (0.262) | 4.85 | <0.001 |
| *Random Effects* | **Std. deviation** | | |
| Family | <0.001 | | |
| Species nested in family | 0.757 | | |
| Site | 0.230 | | |

**Table 3.** Minimum generalized linear mixed effects model for probability of establishment success of seedlings in the first growing season of 20 alien and native rare and common plant species under high and low disturbance treatment and biocide or water control treatment as well as open and closed cages.

| **Parameters** | **Estimate (Std. error)** | **t-value** | **p-value** |
|---|---|---|---|
| *Fixed Effects* | | | |
| Intercept | 1.020 (0.651) | 1.568 | 0.116 |
| Biocide (yes) | 0.343 (0.345) | 0.994 | 0.320 |
| Disturbance (low) | -0.528 (0.343) | -1.538 | 0.124 |
| Origin (native) | 0.064 (0.543) | 0.118 | 0.906 |
| Leaves | 0.436 (0.050) | 8.684 | <0.001 |
| Biocide (yes) : Disturbance (low) | -0.857 (0.486) | -1.761 | 0.078 |
| Biocide (yes) : Origin (native) | -0.199 (0.195) | -1.021 | 0.307 |
| Disturbance (low) : Origin (native) | -0.404 (0.189) | -2.136 | 0.032 |
| Biocide (yes) : Disturbance (low) : Origin (native) | 0.562 (0.268) | 2.097 | 0.036 |
| *Random Effects* | **Std. deviation** | | |
| Family | 0.863 | | |
| Species nested in family | 1.175 | | |
| Site | 0.417 | | |
| Plot nested in site | 0.700 | | |

**Fig. 1.** Probability of establishment success from seeds (± SE) of 20 alien and native common and rare species under high and low disturbance treatment. Black dots (natives) and open white dots (aliens) display means across species for the respective groups, while grey dots indicate raw data means for each of the species. (Note: y-axis on logit scale)

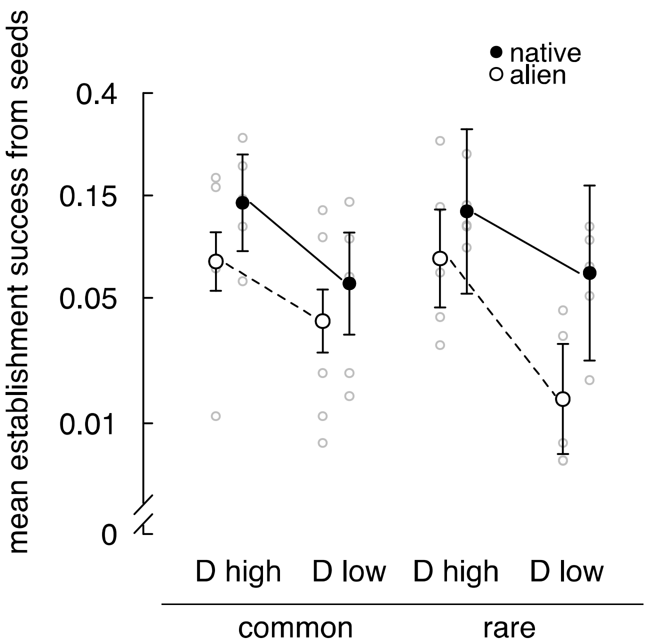


**Fig. 2.** Probability of establishment success from seeds (± SE) of 10 alien and 10 native species under biocide or water control treatment (across species commonness). Black dots display means for native species and open white dots display means for alien species across species across biocide treatments. Grey dots indicate raw data means for each of the species. (Note: y-axis on logit scale)

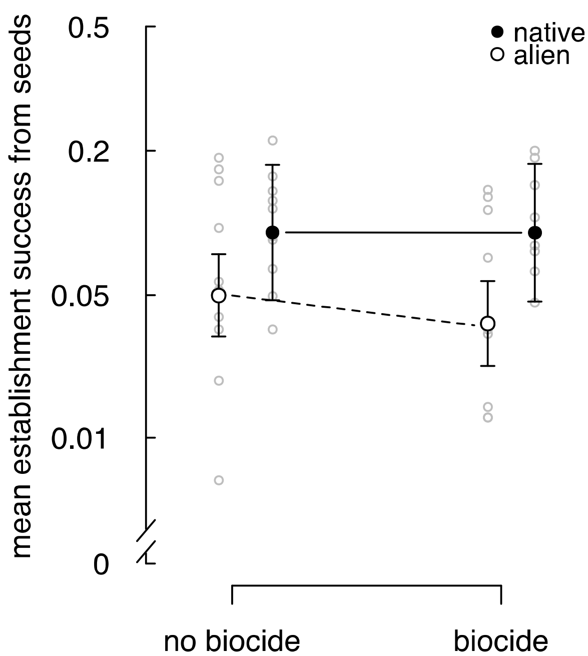


**Fig. 3.** Probability of establishment success from seedlings (± SE) of 10 alien and 10 native species under high and low disturbance and biocide or water control treatment in the 1st growing season. Black dots display means for native species for the respective groups and open white dots display means for alien species (across species commonness). Small grey dots indicate raw data means for each of the species. (Note: y-axis on logit scale)

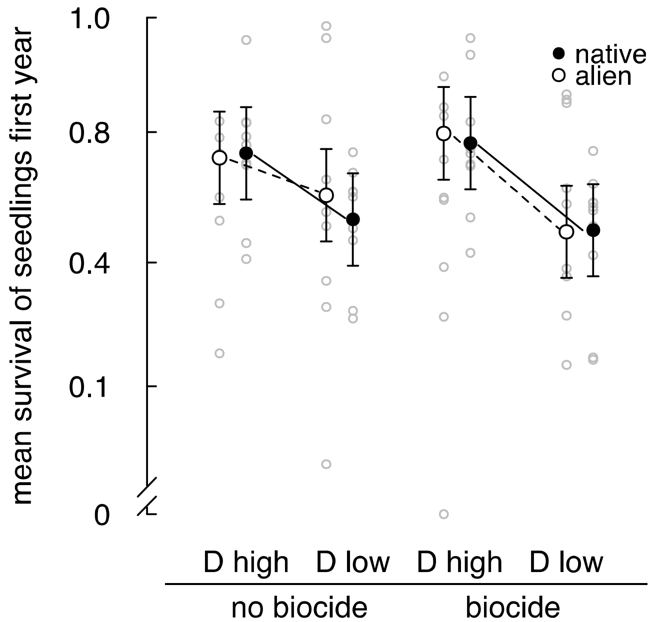
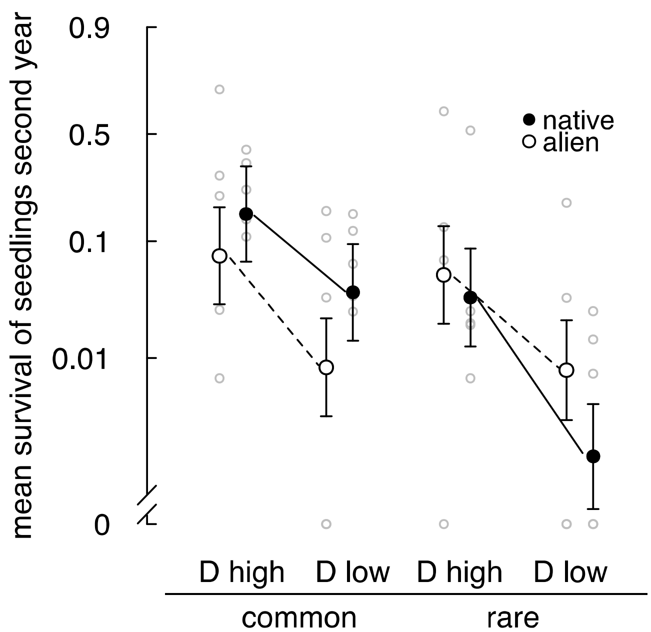


**Fig. 4.** Probability of establishment success from seedlings (± SE) of 10 alien and 10 native common or rare species under high and low disturbance treatment in the 2nd growing season. Black dots display means for native species for the respective groups and open white dots display means for alien species. Small grey dots indicate raw data means for each of the species. (Note: y-axis on logit scale)

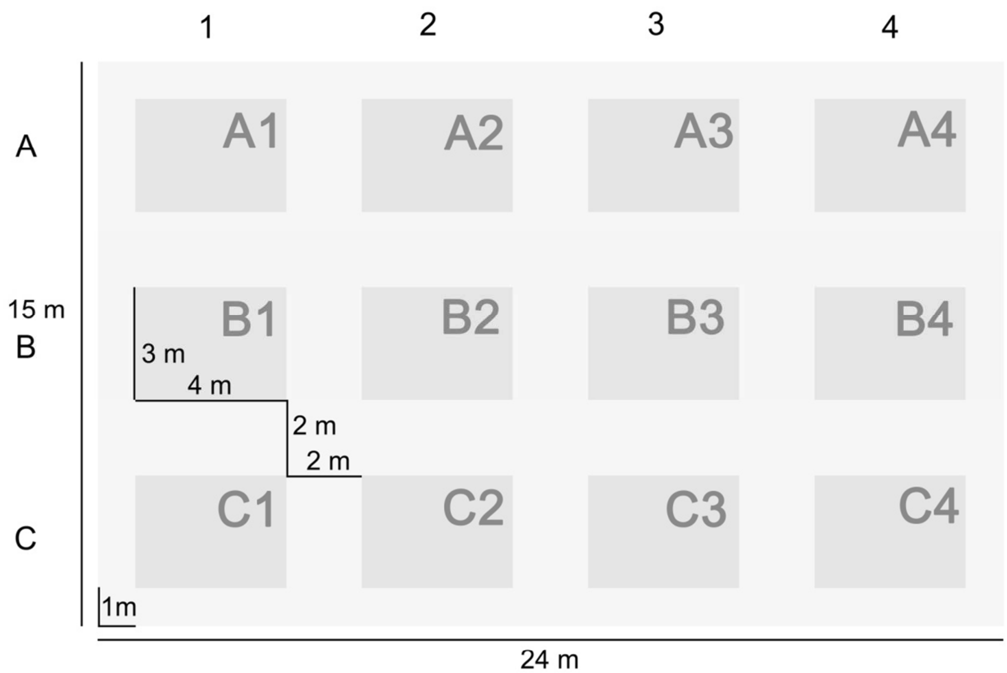


**Appendix S1- Supporting information on experimental setup and model selection**

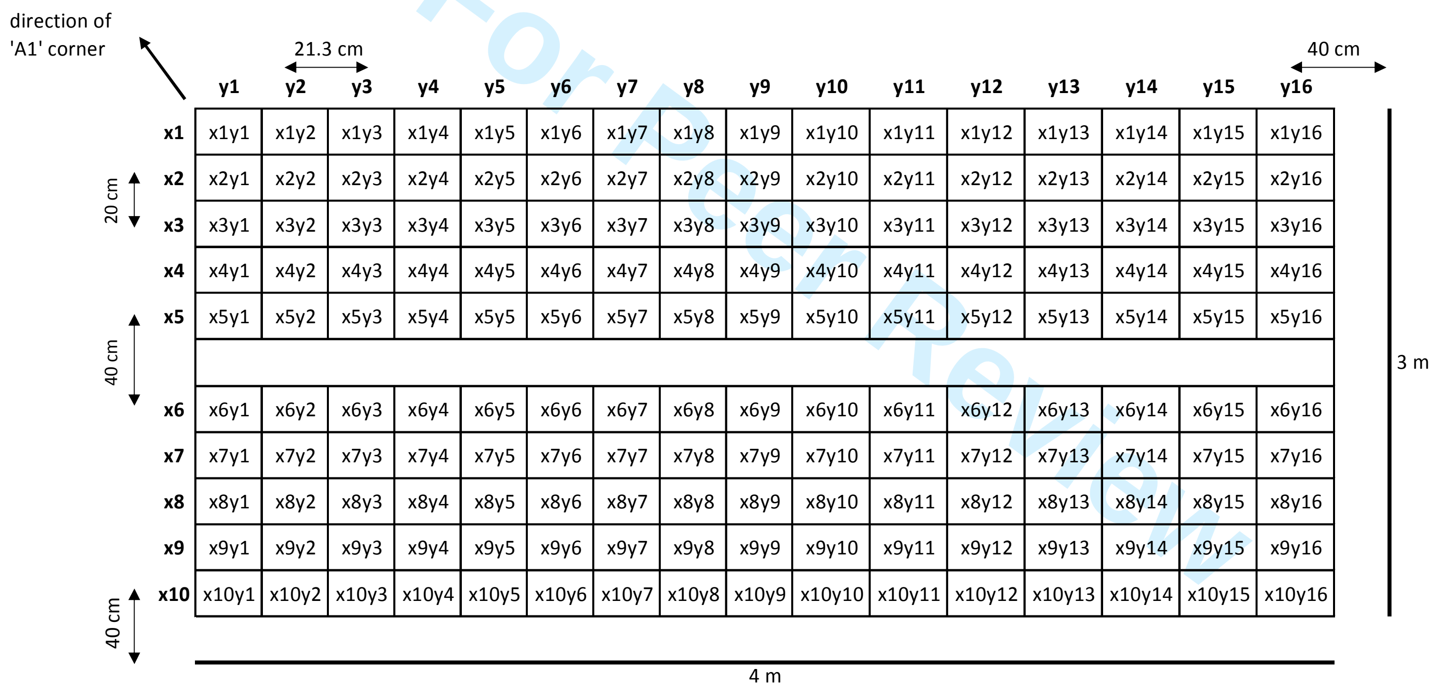
**Appendix S1 Table A1**. Geographic coordinates of the 5 study sites in the vicinity of the University of Konstanz, Germany.

| Site | Lat/Long |
|---|---|
| 1 | 47° 41' 15" N 9° 11' 17" E |
| 2 | 47° 41' 10" N 9° 11' 24" E |
| 3 | 47° 41' 4" N 9° 11' 25" E |
| 4 | 47° 40' 57" N 9° 11' 27" E |
| 5 | 47° 41' 40" N 9° 11' 31" E |

**Appendix S1 Fig. A1**. Schematic figure of the setup for one (out of five) experimental sites. Each of the dark grey rectangles (A1 to C4) represents one of 12 plots (3 × 4 m) per site. Four plots in each site were “seed-experiment” plots and eight plots in each site were “seedling-experiment” plots. Plots were separated by 2 m wide paths.



23 **Appendix S1 Fig. A2.** Schematic layout of one plot (3x4m). Each x/y position defines one planting position in a plot



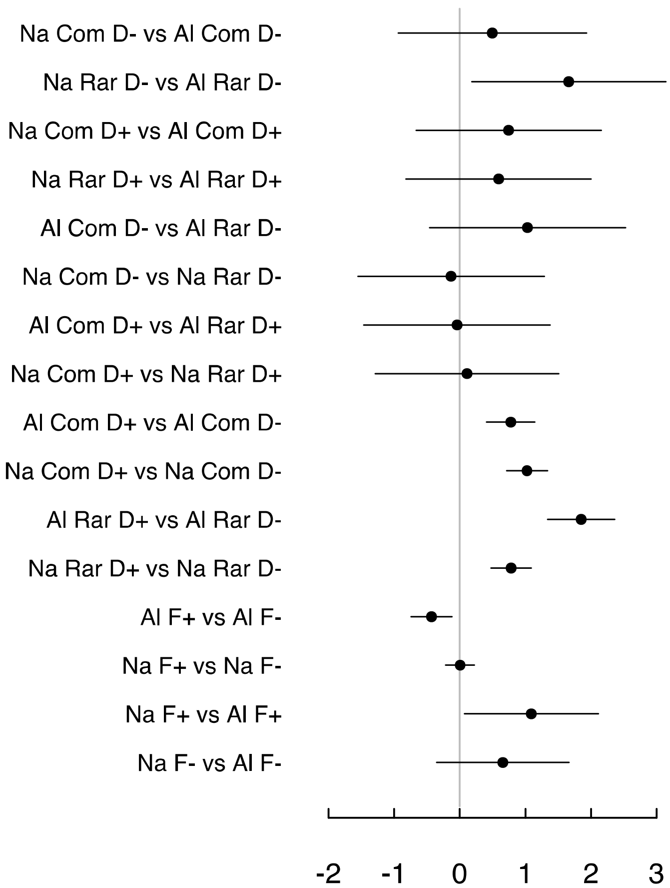
**Appendix S1 Table A2.** Timeline for setup measurements, application of treatments and additional side experiments.

| Tasks | Experiment | Date |
|---|---|---|
| *Setup of sites* | | |
| Identification of resident community | both | 03.04. - 06.04.2014 |
| mowing to 5cm | both | 07.04. - 08.04.2014 |
| tillage | both | 09.04. - 10.04.2014 |
| sowing seeds | seed exp. | 14.04. - 16.04.2014 |
| building of cages | seedling exp. | 01.05. - 20.05.2014 |
| rearing seedlings | seedling exp. | 17.03. - 16.04.2014 |
| planting seedlings | seedling exp. | 17.04. - 29.04.2014 |
| *biocide application* | | |
| 1st biocide application (Previcur En.) | both | 30.04. - 01.05.14 |
| 2nd biocide application (Fenomenal) | both | 11.06.14 |
| 3rd biocide application (Previcur En.) | both | 23.07. - 24.07.2014 |
| 4th biocide application (Fenomenal) | both | 10.09.14 |
| 5th biocide application (Previcur En.) | both | 22.10. - 23.10.2014 |
| 6th biocide application (Fenomenal) | both | 25.03.15 |
| 7th biocide application (only subplots) (Previcur En.) | | 14.05. - 15.05.2015 |
| *Surveys* | | |
| 1st survey (seeds) | seed exp. | 02.06. - 17.06.2014 |
| 2nd survey (seeds - no sufficient data) | seed exp. | 12.04. - 14.04.2015 |
| 1st survey (seedlings) | seedling exp. | 05.05. - 12.05.2014 |
| 2nd survey (seedlings) | seedling exp. | 28.05. - 12.08.2014 |
| 3rd survey (seedlings) | seedling exp. | 16.04. - 24.04.2015 |
| *Additional measures* | | |
| per centage cover | seedling exp. | 23.06. - 27.06.2014 |
| soil samples | both | 22.07.14 |
| setting up subplots (effect on resident community) | side exp. | 24.03.15 |
| harvest of subplots (effect on resident community) | side exp. | 17.06.15 |
| beer traps (cage efficiency meassurement) | seedling exp. | 21.06. - 22.06.2015 |
| insect collection (cage efficiency meassurement) | seedling exp. | 18.06. - 19.06.2015 |
| Plantago root collection (test side effects of biocide) | seedling exp. | 18.06. - 21.06.2015 |

**Appendix S1 Table A3.** Results for each step of the stepwise backward model selection via likelihood-ratio tests for the generalized linear mixed effects model of establishment success of seeds. The main effects that were contained in a significant interaction were not tested, as the interaction was retained in the minimum model.

| **Term** | $\chi^2$ | **df** | **p** |
|---|---|---|---|
| *4-way-interaction* | | | |
| Disturbance x Biocide *x* Origin *x* Commonness | 0.30 | 1 | 0.583 |
| *3-way-interactions* | | | |
| Biocide *x* Origin x Commonness | 0.24 | 1 | 0.624 |
| Disturbance x Biocide x Commonness | 0.56 | 1 | 0.454 |
| Disturbance x Biocide x Origin | 3.54 | 1 | 0.059 |
| Disturbance x Origin x Commonness | 24.16 | 1 | **<0.001** |
| *2-way-interactions* | | | |
| Biocide x Commonness | 0.42 | 1 | 0.516 |
| Disturbance x Biocide | 1.54 | 1 | 0.214 |
| Biocide x Origin | 6.66 | 1 | **0.009** |

**Appendix S1 Fig A3.** Plot with estimates of differences between means and respective 95% confidence intervals for all pairwise comparisons of the terms included in significant interactions in the model for seeds.

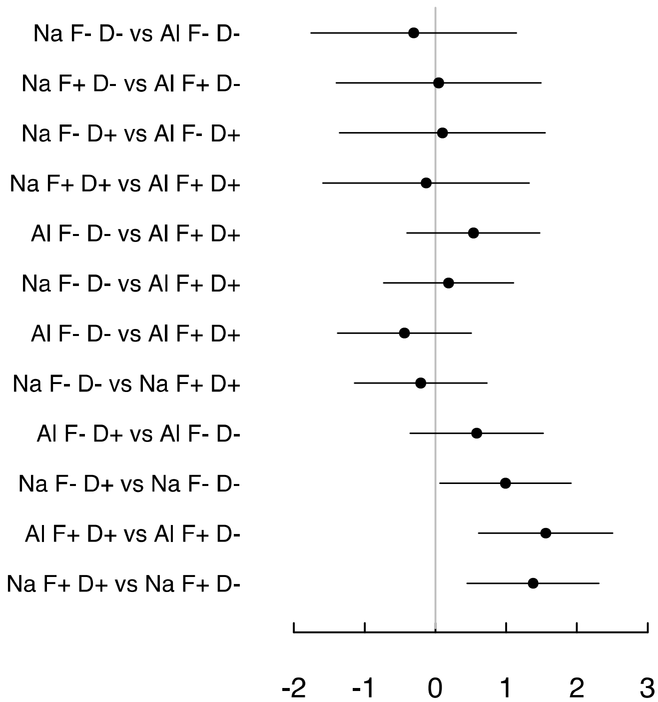


**Appendix S1 Table A4.** Results for each step of the stepwise backward model selection via likelihood-ratio tests for the generalized linear mixed effects model of establishment success of seedlings in the 1st growing season. The main effects that were contained in a significant interaction were not tested, as the interaction was retained in the minimum model.

| **Term** | $\chi^2$ | **df** | **p** |
|---|---|---|---|
| *5-way-interaction* | | | |
| Biocide : Disturbance : Herbivory : Commonness : Origin | 0 | 1 | 0.986 |
| *4-way-interaction* | | | |
| Biocide : Herbivory : Commonness : Origin | 0.007 | 1 | 0.931 |
| Biocide : Disturbance : Herbivory : Origin | 0.064 | 1 | 0.800 |
| Biocide : Disturbance : Commonness : Origin | 0.107 | 1 | 0.743 |
| Disturbance : Herbivory : Commonness : Origin | 1.086 | 1 | 0.297 |
| Biocide : Disturbance : Herbivory : Commonness | 1.485 | 1 | 0.223 |
| *3-way-interaction* | | | |
| Biocide : Herbivory : Commonness | 0.068 | 1 | 0.793 |
| Disturbance : Commonness : Origin | 0.225 | 1 | 0.635 |
| Disturbance : Herbivory : Commonness | 0.63 | 1 | 0.427 |
| Biocide : Commonness : Origin | 0.892 | 1 | 0.345 |
| Biocide : Disturbance : Commonness | 1.061 | 1 | 0.302 |
| Disturbance : Herbivory : Origin | 1.431 | 1 | 0.231 |
| Herbivory : Commonness : Origin | 1.707 | 1 | 0.191 |
| Biocide : Disturbance : Herbivory | 2.529 | 1 | 0.111 |
| Biocide : Herbivory : Origin | 3.001 | 1 | 0.083 |
| Biocide : Disturbance : Origin | 4.370 | 1 | **0.036** |
| *2-way-interaction* | | | |
| Herbivory : Commonness | 0.007 | 1 | 0.933 |
| Herbivory : Origin | 0.032 | 1 | 0.858 |

| | | | |
|---|---|---|---|
| Biocide : Herbivory | 0.125 | 1 | 0.723 |
| Commonness : Origin | 0.185 | 1 | 0.667 |
| Biocide : Commonness | 0.591 | 1 | 0.442 |
| Disturbance : Herbivory | 1.196 | 1 | 0.274 |
| Disturbance : Commonness | 2.895 | 1 | 0.088 |
| *Main effects* | | | |
| Commonness | 1.153 | 1 | 0.282 |
| Height | 2.529 | 1 | 0.111 |
| Herbivory | 3.561 | 1 | 0.059 |
| Leaves | 78.637 | 1 | **<0.001** |

**Appendix S1 Fig A4.** Plot with estimates of differences between means and respective 95% confidence intervals for all pairwise comparisons of the terms included in significant interactions in the model for seedling establishment in the 1st season.



**Appendix S1 Table A5.** Minimum generalized linear mixed effects model explaining probability of seedling establishment success in the 2nd growing season, for 20 alien and native rare and common plant species under high and low disturbance treatment and biocide or water control treatment as well as open and closed cages.

| **Parameters** | **Estimate (Std. error)** | **t-value** | **p-value** |
|---|---|---|---|
| *Fixed Effects* | | | |
| Intercept | -2.266 (1.012) | -2.239 | 0.025 |
| Biocide (yes) | 0.032 (0.333) | 0.096 | 0.923 |
| Disturbance (low) | 2.288 (0.287) | 7.969 | <0.001 |
| Herbivory (open) | -0.279 (0.337) | -0.827 | 0.408 |
| Commonness (rare) | -0.391 (0.746) | -0.524 | 0.600 |
| Origin (native) | 1.059 (0.739) | -1.432 | 0.152 |
| Leaves | 0.621 (0.095) | 6.479 | <0.001 |
| Height | 0.404 (0.067) | 6.015 | <0.001 |
| Biocide (yes) : Herbivory (open) | -0.425 (0.479) | -0.887 | 0.374 |
| Disturbance (low) : Commonness (rare) | 0.334 (0.312) | 1.07 | 0.284 |
| Biocide (yes) : Origin (native) | -0.255 (0.256) | -0.996 | 0.319 |
| Disturbance (low) : Origin (native) | 0.682 (0.271) | 2.517 | 0.011 |
| Herbivory (open) : Origin (native) | -0.612 (0.270) | -2.269 | 0.023 |
| Commonness (rare) : Origin (native) | -1.321 (1.048) | -1.26 | 0.207 |
| Biocide (yes) : Herbivory (open) : Origin (native) | 0.924 (0.383) | 2.414 | 0.157 |
| Disturbance (low) Commonness (rare) : Origin (native) | -1.987 (0.551) | -3.605 | <0.001 |
| | | | |
| *Random Effects* | **Std. deviation** | | |
| Family | 1.644 | | |
| Species nested in family | 1.100 | | |
| Site | 0.187 | | |

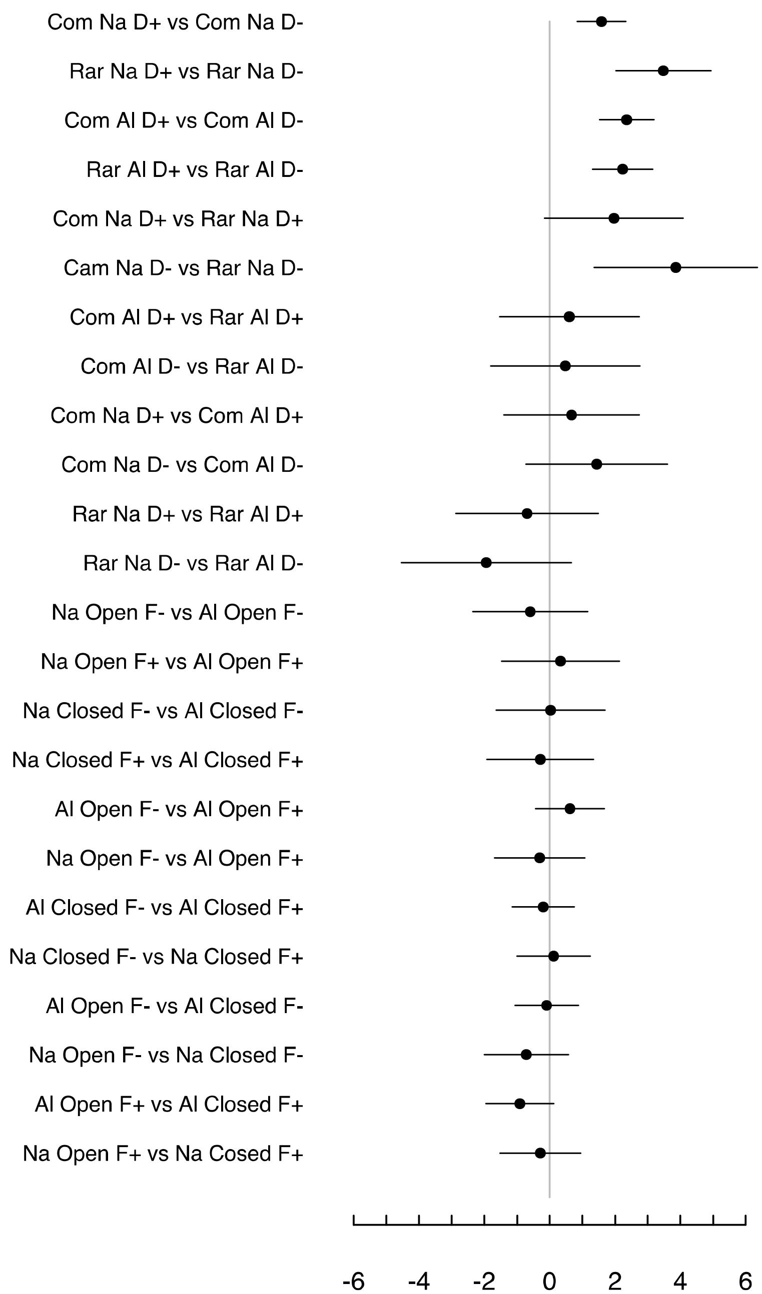
| | |
|---|---|
| Plot nested in site | 0.601 |

**Appendix S1 Table A6.** Results for each step of the stepwise backward model selection via likelihood-ratio tests for the generalized linear mixed effects model explaining establishment success of seedlings in the 2nd growing season. The main effects that were contained in a significant interaction were not tested, as the interaction was retained in the minimum model.

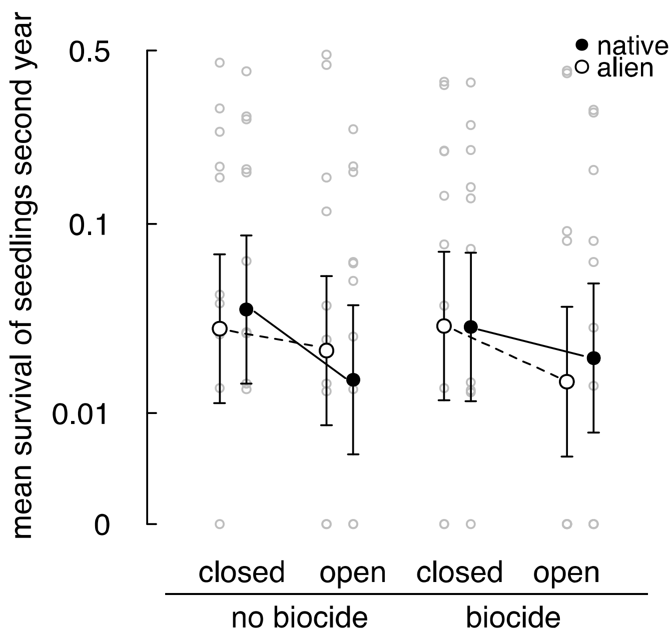
| Term | $\chi^2$ | df | p |
|---|---|---|---|
| *5-way-interaction* | | | |
| Biocide : Disturbance : Herbivory : Commonness : Origin | 0.084 | 1 | 0.772 |
| *4-way-interaction* | | | |
| Biocide : Disturbance : Herbivory : Commonness | 0.340 | 1 | 0.559 |
| Biocide : Disturbance : Commonness : Origin | 0.450 | 1 | 0.502 |
| Biocide : Herbivory : Commonness : Origin | 0.627 | 1 | 0.428 |
| Disturbance : Herbivory : Commonness : Origin | 1.986 | 1 | 0.158 |
| Biocide : Disturbance : Herbivory : Origin | 3.525 | 1 | 0.064 |
| *3-way-interaction* | | | |
| Biocide : Herbivory : Commonness | 0.058 | 1 | 0.809 |
| Disturbance : Herbivory : Commonness | 0.134 | 1 | 0.713 |
| Biocide : Disturbance : Origin | 0.343 | 1 | 0.557 |
| Biocide : Herbivory : Origin | 0.515 | 1 | 0.473 |
| Biocide : Disturbance : Commonness | 1.277 | 1 | 0.258 |
| Biocide : Commonness : Origin | 1.263 | 1 | 0.261 |
| Biocide : Disturbance : Herbivory | 1.973 | 1 | 0.16 |
| Herbivory : Commonness : Origin | 3.262 | 1 | 0.07 |
| Biocide : Herbivory : Origin | 5.723 | 1 | **0.016** |
| Disturbance : Commonness : Origin | 13.957 | 1 | **<0.001** |
| *2-way-interaction* | | | |
| Biocide : Commonness | 0 | 1 | 0.996 |
| Disturbance : Herbivory | 0.114 | 1 | 0.734 |

| | | | |
|---|---|---|---|
| Biocide : Disturbance | 1.428 | 1 | 0.231 |
| Herbivory : Commonness | 3.28 | 1 | 0.07 |
| *Main effects* | | | |
| Leaves(log) | 43.507 | 1 | **<0.001** |
| Height | 34.916 | 1 | **<0.001** |

**Appendix S1 Fig A5.** Plot with estimates of differences between means and respective 95% confidence intervals for all pairwise comparisons of the terms included in significant interactions in the model for seedlings in the 2nd season.



**Appendix S1 Fig. A6.** Probability of establishment success from seedlings (± SE) of 10 alien and 10 native species in open and closed cages under biocide or water control treatment in the 2nd growing season. Black dots display means for native species for the respective groups and open white dots display means for alien species. Small grey dots indicate raw data means for each of the species. (Note: y-axis on logit scale).



**Appendix S1 Table A7** Minimum generalized linear mixed effects model explaining seedling relative change in plant size of 20 alien and native rare and common plant species under high and low disturbance treatment and biocide or water control treatment as well as open and closed cages.

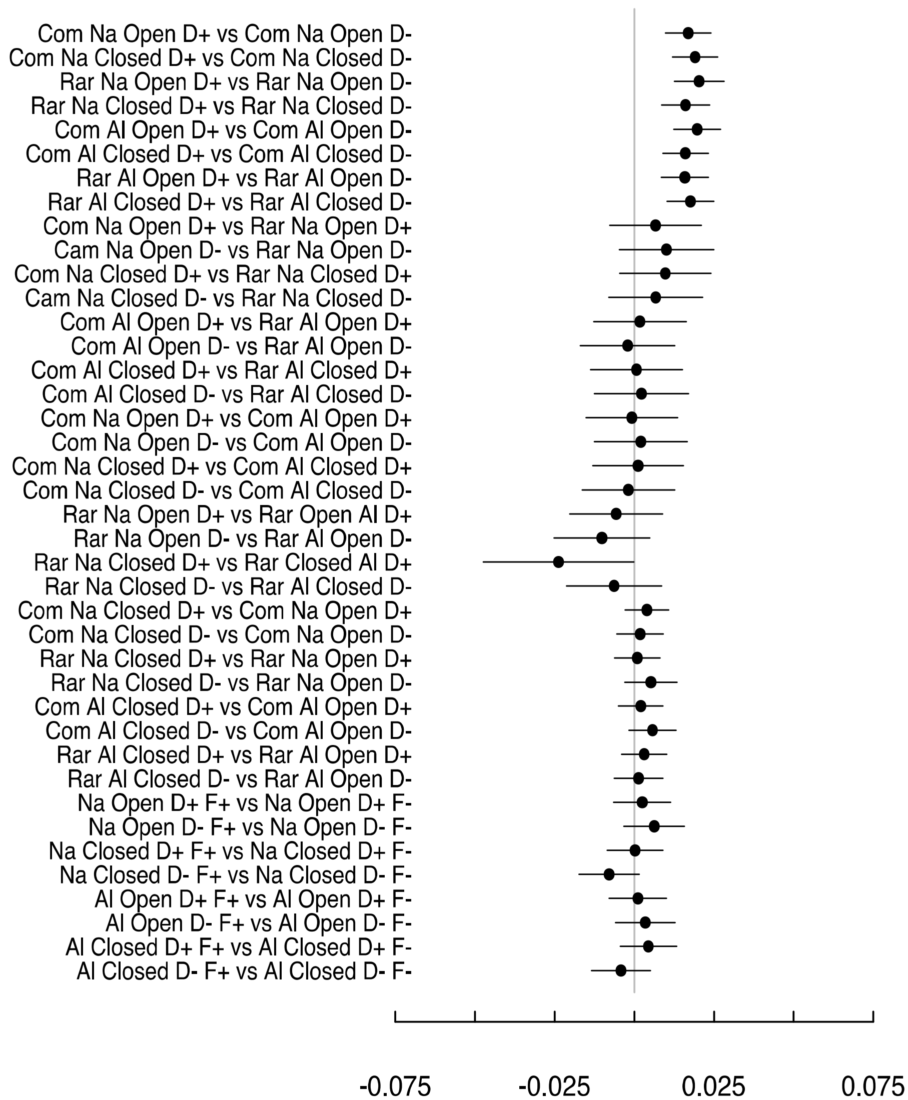
| **Parameters** | **Estimate (Std. error)** | **t-value** |
|---|---|---|
| *Fixed Effects* | | |
| Intercept | 0.023 (0.007) | 3.167 |
| Biocide (yes) | 0.004 (0.002) | 1.597 |
| Disturbance (low) | -0.011 (0.002) | -4.002 |
| Herbivory (open) | -0.000 (0.002) | -0.087 |
| Commonness (rare) | -0.000 (0.004) | -0.167 |
| Origin (native) | 0.003 (0.004) | 0.674 |
| Biocide (yes) :Disturbance (low) | -0.008 (0.003) | -2.232 |
| Biocide (yes) : Herbivory (open) | -0.003 (0.003) | -0.916 |
| Disturbance (low) : Herbivory (open) | -0.009 (0.004) | -2.247 |
| Disturbance (low) : Commonness (rare) | -0.001 (0.002) | -0.718 |
| Herbivory (open) : Commonness (rare) | -0.001 (0.001) | -0.521 |

| | | |
|---|---|---|
| Biocide (yes) : Origin (native) | -0.003 (0.001) | -2.551 |
| Disturbance (low) : Origin (native) | -0.003 (0.002) | -1.549 |
| Herbivory (open) : Origin (native) | -0.004 (0.002) | -2.180 |
| Commonness (rare) : Origin (native) | -0.009 (0.006) | -1.424 |
| Biocide (yes) : Disturbance (low) : Herbivory (open) | 0.011 (0.005) | 2.146 |
| Disturbance (low) : Herbivory (open) : Commonness (rare) | 0.005 (0.003) | 1.781 |
| Biocide (yes) : Herbivory (open) : Origin (native) | 0.005 (0.002) | 2.638 |
| Disturbance (low) : Herbivory (open) : Origin (native) | 0.005 (0.002) | 2.023 |
| Disturbance (low) : Commonness (rare) : Origin (native) | 0.004 (0.004) | 1.573 |
| Herbivory (open) : Commonness (rare) : Origin (native) | 0.004 (0.002) | 1.522 |
| Disturbance (low) : Herbivory (open) : Commonness (rare) : Origin (native) | -0.012 (0.004) | -2.757 |
| | | |
| *Random Effects* | **Std. deviation** | |
| Family | <0.001 | |
| Species nested in family | <0.001 | |
| Site | <0.001 | |

**Appendix S1 Table A8.** Results for each step of the stepwise backward model selection via likelihood-ratio tests for the generalized linear mixed effects model of relative change in plant size between the 1st and 2nd survey. The main effects that were contained in a significant interaction were not tested, as the interaction was retained in the minimum model

| Term | $\chi^2$ | df | p |
|---|---|---|---|
| *5-way-interaction* | | | |
| Biocide : Disturbance : Herbivory : Commonness : Origin | 0.165 | 1 | 0.684 |
| *4-way-interaction* | | | |
| Biocide : Disturbance : Herbivory : Origin | 0.085 | 1 | 0.77 |
| Biocide : Disturbance : Commonness : Origin | 0.123 | 1 | 0.725 |
| Biocide : Disturbance : Herbivory : Commonness | 0.598 | 1 | 0.439 |
| Biocide : Herbivory : Commonness :Origin | 2.168 | 1 | 0.14 |
| Disturbance : Herbivory : Commonness :Origin | 7.619 | 1 | **0.005** |
| *3-way-interaction* | | | |
| Biocide : Commonness : Origin | 0.103 | 1 | 0.748 |
| Biocide : Disturbance : Origin | 0.225 | 1 | 0.634 |
| Biocide : Disturbance : Commonness | 0.316 | 1 | 0.573 |
| Biocide : Herbivory : Commonness | 1.7 | 1 | 0.192 |
| Biocide : Disturbance : Herbivory | 5.312 | 1 | **0.211** |
| Biocide : Herbivory : Origin | 7.013 | 1 | **0.008** |

**Appendix S1 Fig A7**. Plot with estimates of differences between means and respective 95% confidence intervals for all pairwise comparisons of the terms included in significant interactions in the model explaining seedling relative change in plant size.



## Appendix S2 - Additional experiments to test for the effects of the applied treatments

*Disturbance effects on plant cover*

To assess the effects of the disturbance treatment, we recorded percentage cover of plants and bare ground in a 20 cm x 20 cm square centered on each target position in the seedling experiment. We analysed percentage of bare ground using a linear mixed model in lme4 (Bates et al. 2014). The percentage data were arc sin square root transformed to achieve normality of the data. Disturbance, biocide treatment and herbivory reduction treatment and all respective interactions were included as explanatory variables in the model. Site and plot nested in site were included as random effects, and likelihood-ratio tests were performed to assess significance of the model terms.

The disturbance treatment had a significant effect on percentage bare ground ($\chi^2$ = 32.77, df = 1, P < 0.001). High disturbance plots had 34.2% bare ground on average compared to 19.4% in low-disturbance plots. This indicates that the disturbance treatment was effective in regard to removal of resident plants (i.e. competitors for incoming species).

*Disturbance effects on nutrient availability*

Soil samples were taken in the middle of each plot using a soil corer with 5 cm diameter to a depth of approximately 8 cm. The soil samples were stored at -80° C immediately after collecting until further processing. Leaf and root material was removed from defrosted soil samples, which were then sieved (2-mm mesh). We added 20 g of soil to 80 ml of 0.0125 M $CaCl_2$ (1:4 soil/salt-solution). These suspensions were put for 2 h on an orbital shaker (speed dial 120). Then we left them to settle for 1 minute, poured the suspension through a filter paper (Whatman 595 ½, 70mm filter paper, GE Healthcare) and froze the filtrate until nitrogen-availability analysis. The total nitrate and nitrite concentration ($NO_2^-$ and $NO_3^-$ in µg/g dry soil) of the filtrate was analyzed using a segmented flow auto-analyzer (Technicon® AutoAnalyzer II, Technicon®). Per sample, 4 ml was analyzed.

We analyzed $NO_2^-/NO_3^-$ concentration using a linear mixed model with lme4. Disturbance, biocide treatment and herbivory-reduction treatment, as well as all possible interactions were used as model terms, and site was used as a random effect. We used likelihood ratio tests to assess the significance of the model terms.

None of the model terms had a significant effect on the $NO_2^-/NO_3^-$ concentration of the soil. This indicates that none of our treatments significantly altered the nutrient availability for the plants.

*Biocide effects on resident community*

To test the effect of the biocides on the resident community, we installed one pair of 30 x 30 cm subplots ("block") on three sides of each site in the 1 m strips around the plots at the beginning of the growing season in the second year (Appendix S1 Table A3). We treated one subplot in each pair once with each of the two biocides (same concentrations as the biocide treatment of the experimental plots; 1st application Fenomenal®, 2nd application Previcur Enegy®), whereas the other one received the same amounts of water as a control. We harvested the biomass of the subplots on the 17th of June 2015, dried the samples at 80°C for 48 h and weighed them to assess the performance of the resident community with and without biocide application.

We analysed the total biomass of the subplots treated with and without biocide using a generalized linear mixed model in lme4 (Bates et al. 2014). Biomass data was natural-log transformed to achieve normality. Biocide treatment (with/without) was included as a fixed effect. Block nested in site was included as a random effect. A likelihood-ratio test was performed to assess significance of biocide treatment.

Subplots treated with biocide had a slightly larger biomass (mean= 3.737, SE = ±0.086) than the control plots (mean= 3.608, SE = ±0.086), however, this effect was marginally non-significant ($\chi^2 = 2.76$, df = 1, P = 0.095).

*Mycorrhiza analysis*

To test for any potential side effects of the biocide treatment on mycorrhization of plants we also collected roots of three *Plantago lanceolata* plants (growing in sufficient numbers in all plots – therefore used as a bioassay) in each of the plots in all five sites. We washed the roots and heated them at 80°C in a 10% KOH solution in a water bath until the roots became transparent. After that, the roots were heated again for five minutes in a 5 % vinegar, 5 % ink solution (Parker Quink Black, NWL France Services, Boulogne, France) to stain mycorrhizal fungal structures. We mounted the stained roots on glass slides, and analysed them by counting mycorrhizal fungal structures (vesicles, arbuscules and hyphae) at 50 intersections per sample under a microscope at 100x magnification (Zeiss Axioscope, Carl Zeiss, Jena Germany).

We analysed the number of intersections containing mycorrhiza fungal structures or not, using binomial generalized linear mixed models in the lme4 package. We used separate models for “seed” and “seedling” plots. The model for the “seed plots” contained the fixed factors biocide and disturbance as well as the interaction between both. Site, and plot nested in site were added as random effects. The model for the “seedling plots” was the same, but additionally contained herbivory treatment as a fixed term as well as all possible interactions with it. We used likelihood ratio tests to determine the significance of the model terms.

*Plantago lanceolata* roots from high disturbance "seed plots" showed a lower rate mycorrhizal colonisation (high disturbance mean= -0.294, SE = ±0.143, low disturbance mean= 0.215, SE = ±0.1014; $\chi^2$ = 3.832, df = 1, P = 0.050). *Plantago lanceolata* roots in the seedling plots did not show any significant differences in mycorrhizal colonisation between treatments.

*Effectiveness of herbivore-reduction treatment*

To assess the effectiveness of the cages in regard to herbivore reduction, we set up beer traps in the open cages on the 21$^{st}$ of June 2015 (i.e. in the 2$^{nd}$ season), in addition to the beer traps that we had already in the closed cages. We filled all traps with beer (Fürstenbergische Brauerei, Donaueschingen, Germany), and counted the slugs found in the traps of open and closed cages on the following day.

To assess whether there were differences in arthropod abundance in the open and closed cages, we used a vacuum suction device (Type LB37CCM, ECON Handel, Herzebrock-Clarholz, Germany) to collect arthropods. We used the vacuum suction device for five minutes in every plot. We performed the arthropod sampling between the 18$^{th}$ and 19$^{th}$ of June 2015. The collected arthropods were put in a -80°C freezer for five minutes and were then classified according to their mode of feeding into groups of herbivores, omnivores and non-herbivores.

We analysed the number of slugs, the number of herbivorous arthropods and the total number of arthropods per plot using negative binomial generalized linear mixed models in the glmmADMB package (Fournier et al. 2012). We included herbivore treatment (open cages/closed cages) as a fixed effect and site as a random effect in the model. As for the other analyses, we used a likelihood-ratio test to determine the significance of the fixed effect.

Compared to the open cages, the closed cages had significantly fewer slugs (open: mean= 3.874, 95% CI = ±0.250, closed: 1.689, SE = ±0.266; $\chi^2$ = 91.01, df = 1, P < 0.001), herbivorous arthropods (open: 2.829, SE = ±0.151, closed: 2.230, SE = ±0.159; $\chi^2$ = 10.26, df = 1, P = 0.001) and total arthropods (open: 4.326, SE = ±0.193, closed: 3.457, SE = ±0.195; $\chi^2$ = 10.26, df = 1, P = 0.001).

**Appendix S3 – Additional analysis excluding the Onagraceae**

Due to high mortality over the winter and differences in survival between the species, a large proportion of surviving plants were from a single family - the Onagraceae. Thus, to test the robustness of the results, we also analysed the survival in the 2nd growing season excluding the Onagraceae using the same procedure as for the full data set.

The minimum model excluding the Onagraceae contained a significant three-way interaction between herbivory treatment, species commonness and origin ($X^2 = 4.606$, df = 1, P = 0.031, Table C1). This interaction showed that common native species survived significantly less well in open cages than in closed cages (mean difference = -1.292, SE = ±0293, P <0.001, Fig. C1), while common natives survived significantly more than rare natives in both open (2.494, SE = ±0.852, P =0.038, Fig. C1) and closed cages (3.143, 95% CI = ±0.761, P <0.001, Fig. C1). These differences were not observed for the non-Onagraceae aliens. Furthermore, the minimum model contained the significant main effects of plant height ($X^2 = 31.915$, df = 1, P < 0.001, Table C1) and number of leaves ($X^2 = 23.412$, df = 1, P < 0.001,Table C1), as well as disturbance ($X^2 = 27.726$, df = 1, P < 0.001, Table C1). These findings indicate that larger plants showed a higher survival and that disturbance also increased survival regardless of species origin or commonness (1.640, SE = ±0.316, P <0.001)

**Appendix S3 Table C1.** Minimum generalized linear mixed effects model for probability of establishment success of seedlings in the second growing season of 16 alien and native rare and common plant species (excluding the Onagraceae family) under high and low disturbance treatment and biocide or water control treatment as well as open and closed cages.

| **Parameters** | **Estimate (Std. error)** | **t-value** | **p-value** |
|---|---|---|---|
| *Fixed Effects* | | | |
| Intercept | -3.210 (0.965) | -3.326 | <0.001 |
| Disturbance (low) | 1.592 (0.260) | -6.123 | <0.001 |
| Herbivory (open) | -1.008 (0.318) | -3.168 | 0.002 |
| Commonness (rare) | -0.083 (0.0.852) | -0.098 | 0.921 |
| Origin (native) | 1.749 (0.816) | 2.142 | 0.032 |
| Leaves | 0.587 (0.122) | 4.780 | <0.001 |
| Height | 0.459 (0.079) | 5.796 | <0.001 |
| Herbivory (open) : Commonness (rare) | -0.960 (0.478) | -2.007 | 0.044 |
| Herbivory (open) : Origin (native) | -0.478 (0.308) | -1.554 | 0.120 |
| Commonness (rare) : Origin (native) | -2.583 (1.207) | -2.140 | 0.032 |
| Herbivory (open) : Commonness (rare) :Origin (native) | 1.707 (0.744) | 2.294 | 0.021 |
| *Random Effects* | **Std. deviation** | | |
| Family | 1.237 | | |
| Species nested in family | 1.095 | | |
| Site | 0.245 | | |
| Plot nested in site | 0.618 | | |

**Appendix S3 Fig. C1**.Probability of establishment success from seedlings (± SE) of 8 alien and 8 native common and rare species in open and closed cages in the 2nd growing season, excluding the Onagraceae family. Black dots display means for native species for the respective groups and open white dots display means for alien species. Small grey dots indicate raw data means for each of the species. (Note: y-axis on logit scale)